

A NEW MARINE CERCARIA FROM THE WOODS HOLE REGION
AND ITS BEARING ON THE INTERPRETATION OF LARVAL
TYPES IN THE FELLODISTOMATIDAE
(TREMATODA: DIGENEA)

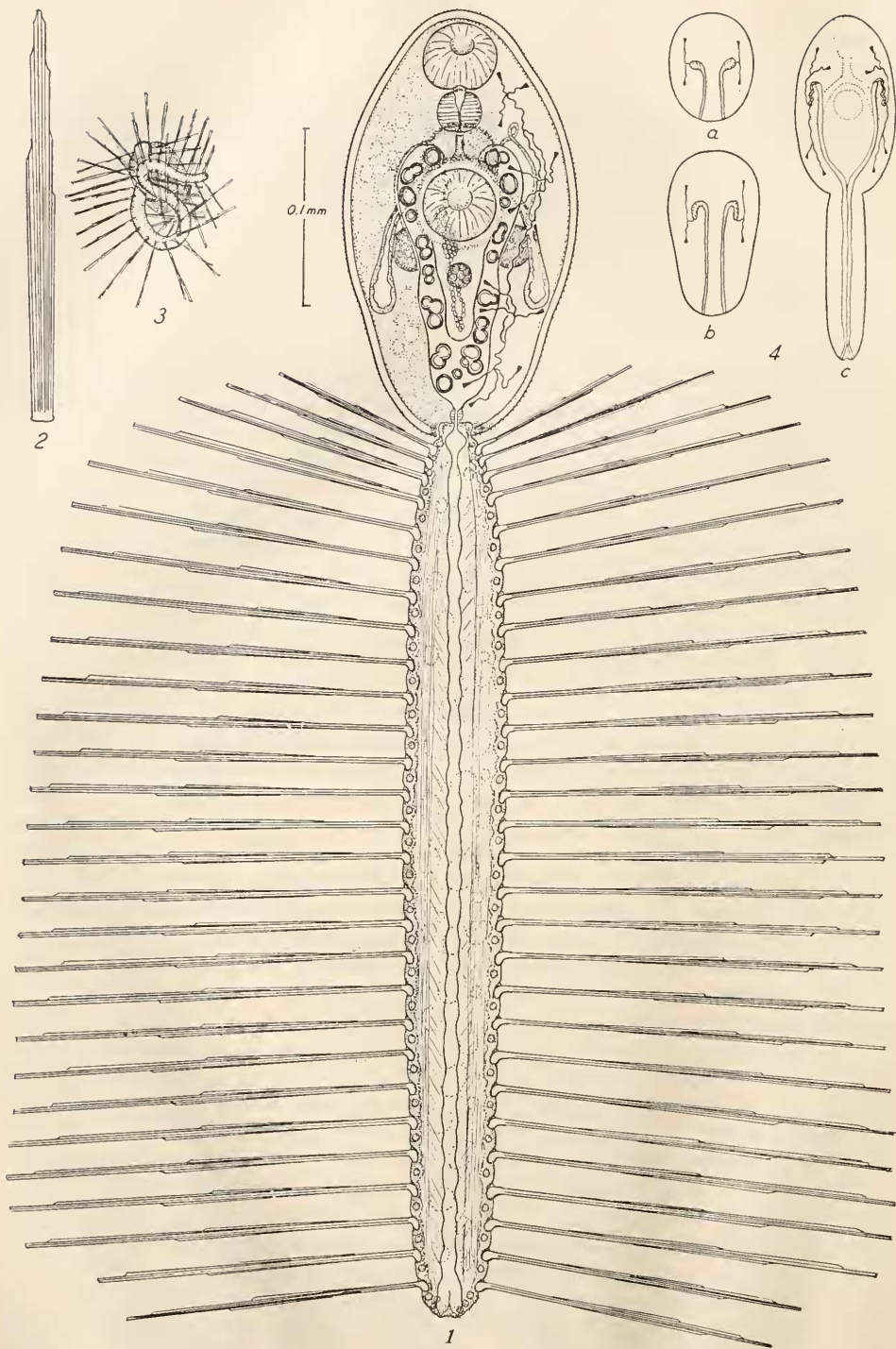
R. M. CABLE

*Department of Biological Sciences, Purdue University, Lafayette, Indiana, and
The Marine Biological Laboratory, Woods Hole, Mass.*

The concept of two great groups of digenetic trematodes as proposed by La Rue (1926) is based in part on the type of cercaria which is furcocercous in the order Strigeatoidea and non-furcocercous in the order Prosostomata. However, the tails of cercariae are subject to such varied and extreme modifications in many instances as to give little indication of the basic type. Unfortunately, the pioneering life history studies in some families concerned species having just such extremely modified larvae and hence did not reveal fundamental relationships, a knowledge of which has had to await investigations dealing with more "typical" representatives. Excellent examples of groups in which this situation has proved to be the case are the families Brachylaemidae and Fellodistomatidae.

In the Fellodistomatidae, the first life history to be reported was that of *Bacciger bacciger* which according to Palombi (1934) has a trichocercous cercaria with a non-bifid tail. Subsequent studies have shown that at least some fellodistomatids have furcocercous larvae as discussed in a recent paper (Cable, 1953) which should have taken into account also the life cycle of *Fellodistomum fellis* as described by Chubrick (1952). In reporting for that species a furcocercous larva developing in marine lamellibranchs, her observations lend further confirmation of the view that the Fellodistomatidae properly belong in the order Strigeatoidea. This view poses no difficulty in the interpretation of caudal structure of many fellodistomatid cercariae in which the tail is reduced or even absent. Such instances obviously are examples of caudal reduction associated with the abbreviation of free-living activity now recognized to occur in various distantly related families. It is this modification that has led to classifying larval trematodes into such unnatural categories as *Microcercous Cercariae* and *Cercariaca*.

The interpretation of the cercaria of *Bacciger bacciger* and similar larvae in respect to the furcocercous type is quite another matter. In such larvae, the tail is well developed without possessing furcae and has paired lateral setaceous tufts, the elements of which may be joined by delicate webbing to form finlets. Such a larva was among the fellodistomatid cercariae found by the writer in Puerto Rico and figured in a recent paper (Cable, 1953). That cercaria was found in but one clam, before the other larvae included in that paper were seen and hence before the significance of determining the precise relationship of the excretory system to the tail was appreciated. Fortunately, the writer was aware that a very similar cercaria occurs in the Woods Hole region and a brief visit to that area was made during the summer of 1953 to study the species. It was quickly found, thanks to Prof. P. S. Crowell, Jr. and students of the Invertebrate Zoology class



EXPLANATION OF PLATE I
(All figures concern *Cercaria laeviscardii*)

through whose assistance over 200 specimens of the clam serving as the host were made available. As the larva has not yet been reported, it is here described and named after the host.

Specific diagnosis: distome, non-ocellate, trichocercous cercaria developing in simple sporocysts in the visceral mass of a marine lamellibranch. Body of cercaria yellowish in life, tail with 28 pairs of slender, lateral finlets, each composed of setae, usually 10 in number, united by a delicate web; finlets shorter at each end of tail and closer together at its proximal end. Associated with bases of finlets on each side is a uniform row of similar nuclei which are prominent in stained specimens. Dorsal and ventral caudal fins are absent; tail widest at about mid-length and rather blunt posteriorly. Entire body and tail finely spinose, cuticle of body thick and with fine striae. Suckers about equal with the ventral sucker embedded in a prominent protrusion somewhat anterior to mid-level of body and overhanging a ventral depression of the fore body. Oral sucker not at extreme anterior end of body, with the mouth opening ventrally. Prepharynx extremely short, pharynx well developed, esophagus about as long as pharynx and receiving just anterior to ventral sucker the ceca which reach about halfway between ventral sucker and posterior end of body; ceca thick-walled and with somewhat inflated blind ends. Cephalic and cystogenous glands not evident. Primordia of reproductive system well developed; testes dorsal, symmetrical, and just posterolateral to ventral sucker; ovary more ventral, median, and just posterior to level of testes; other primordia are represented by strands of nuclei and a prominent mass posterodorsal to ventral sucker. Excretory vesicle U- or almost V-shaped, with wide arms extending anterior to ventral sucker and with large, refractile concretions. From each arm of the excretory vesicle, a ciliated recurrent tubule extends posteriorly to about mid-level of body and receives an anterior and a posterior collecting tubule, each of which is joined by two groups of flame cells, three cells per group. The excretory formula is accordingly $2 [(3 + 3) + (3 + 3)] = 24$ flame cells. A distinct bladder sphincter is present and from it the prominent caudal excretory tubule extends the length of the tail, bifurcating just before reaching the pair of embryonic excretory pores at the posterior tip of the tail. Measurements in millimeters of cercariae killed in hot sea water, mounted without pressure, and selected for specimens showing a minimum of body flexure are as follows: body length 0.185–0.243, maximum body width 0.10–0.13; tail 0.426–0.517 long and 0.050–0.054 in maximum width exclusive of appendages. Caudal finlets range in length from 0.095 near base of tail to a maximum of about 0.30 elsewhere. Oral sucker 0.035–0.040 in diameter, usually a little wider than long; ventral sucker 0.038–0.040 and pharynx 0.022–0.025 in diameter. Sporocysts elongate, young ones with pointed ends which are very motile; older sporocysts up to 3.0 in length, rounded or truncate posteriorly and with a pointed anterior end bearing a terminal birth pore.

FIGURE 1. Entire cercaria in ventral view, drawn to scale from a heat-killed specimen with internal structures added from observations on living and stained larvae.

FIGURE 2. Detail of caudal finlet.

FIGURE 3. Sketch of cercaria to show resting attitude near surface of water.

FIGURE 4. Embryology of the excretory system.

Host: *Laevicardium murtoni* Conrad.

Locality: Lagoon Pond, Martha's Vineyard, Massachusetts.

Incidence of infection: 25–33% of clams collected in August, selected for large size, and opened for examination.

Although over 200 clams were isolated in bowls of sea water for 48 hours, no cercariae emerged spontaneously. In some of the clams then opened, the infection was immature but from the visceral mass of others, large numbers of evidently fully developed cercariae escaped and remained alive over 24 hours. They swam energetically, tail-first with the body bent ventrally on the base of the tail. The larvae made rapid progress, often swimming somewhat erratically in one direction and then spinning around before coming to rest near the surface of the water with the body downward and the tail contracted into a coiled mass (Fig. 3). During rest periods, which were frequent, the body would contract and expand and on several occasions cercariae were observed creeping upside down in an inch-worm fashion with the suckers attached to the surface film. No photactic behavior was observed.

Several species of cercariae resembling *C. laevicardii* have been described, mostly by earlier workers whose accounts are so inadequate that a critical evaluation of them is impossible. Dollfus (1925) gave a summary of trichocercous larvae known at that time, dividing marine species into two groups, one in which eye-spots are present, and one in which they are absent. Subsequent studies have revealed that such a distinction may be an artificial one, for instances are known in which one cercaria may be ocellate whereas another larva in the same family lacks eye-spots. On the basis of known life histories, it is certain that the trichocercous cercariae listed by Dollfus have adults belonging to at least three distinct families, the Lepocreadiidae, the Monorchiidae, and the Fellodistomatidae. Furthermore, the last two groups and perhaps all three have some larvae that are not trichocercous. Thus in distinguishing the larvae of these families, the morphology of the body and type of molluscan host are more dependable than is the structure of the tail which can be positively misleading. Of the non-ocellate cercariae listed by Dollfus, *C. setifera* Müller *nec* Monticelli (the larva of *Bacciger bacciger* according to Palombi, 1934), *C. villoti*, *C. pelsenceri*, *C. chiltoni*, and *C. pectinata* Huet *nec* Chilton may be assigned to the Fellodistomatidae. *C. laevicardii* evidently differs from all of these in at least one of the following respects: size of body, tail and suckers; proportionate length of body and tail; and number of setaceous tufts. Among the ocellate cercariae listed by Dollfus, it seems highly probable that *C. elegans* Müller also is a larva of the Fellodistomatidae although the molluscan host is unknown. In a personal communication, Prof. G. R. La Rue has informed the writer of what evidently is an ocellate fellodistome larva taken in plankton from Lake Pontchartrain, Louisiana.

The development of the excretory system provides an interpretation of *Cercaria laevicardii* and similar larvae in respect to the furcocercous type with which they obviously are closely related. In young embryos (Fig. 4), each definitive excretory tubule terminates with a ciliated largement which is joined by capillaries from two flame cells. With further development, four flame cells are seen on each side and this pattern persists until the embryo is well advanced. As the tail develops, the definitive tubules extend its full length to open posteriorly and at about the time

the caudal finlets first appear as small knobs, the tip of the tail shows a tiny but distinct notch separating two short, terminal papillae with the excretory pores at their tips. A faint suggestion of this condition is evident in the fully developed cercaria. After the caudal tubules fuse, the resulting excretory canal is large and conspicuous, just as in furcocercous larvae of the Fellodistomatidae.

From these observations and other studies, it seems evident that larvae of the Fellodistomatidae are basically furcocercous and show at least three types of modification: (1) symmetrical reduction of the entire tail until in some forms it has become a mere knob of cells or lost altogether; (2) disappearance of the furcae without a corresponding reduction of the tail stem; and (3) reduction of the stem only, with the furcae becoming greatly elongate. The first type of modification has a counterpart in other trematode families such as the Brachylaemidae which is closely related to the Fellodistomatidae and the Microphallidae and Monorchidae which are not. In all such cases, caudal modification is associated with reduction or suppression of free-swimming activity of the cercarial stage. However, such an adaptation cannot explain the second type of modification in which the development of finlets from paired lateral setaceous tufts makes the tail an exceedingly effective natatory organ but no more so than in trichofurcocercous species. The third type of modification is exemplified by the unnamed cercaria described by Jones and Rothschild (1932). That larva develops in a marine bivalve, *Nucula nucleus*, and has a tail with an extremely short stem and long, slender furcae which are very extensile. From the structure and host relationship of that cercaria as interpreted in the light of recent studies, there seems no doubt that its adult is a member of the Fellodistomatidae.

Caudal modifications shown by cercariae of the Fellodistomatidae may have considerable phylogenetic significance. Jones and Rothschild (1932) observed that the cercaria from *N. nucleus* superficially resembled bucephalid larvae. That this resemblance may be significant is indicated by the papers of Allison (1943) and Cable (1953) who presented evidence that the Brachylaemidae, Fellodistomatidae and Bucephalidae may form a related group within the Strigeatoidea.

Life history studies of the last two decades have supported and greatly extended La Rue's (1926) concept of two orders of digenetic trematodes, the Strigeatoidea and the Prosostomata. Without exception, it has been found that the definitive excretory pores of cercariae in the Strigeatoidea are posterior in location, at or near the tips of the furcae when present, although secondary openings nearer the body may develop later as in the Bucephalidae. This position of the excretory pores is characteristic also of the rediae and sporocysts in at least some families of the Strigeatoidea. The most striking example of this situation is provided by the family Bivesiculidae in which Le Zotte (1954) has found that the cercariae are furcocystocercous and produced in rediae in which not only is the posterior end cleft but also the excretory pores are at the tips of the resulting lobes just as they are at the tips of the furcae in the cercarial stage. Furthermore, the excretory patterns of the redia and cercaria differ only in respect to the number of flame cells in certain groups, the number of flame cell groups being the same in both stages.

On the other hand, the location of the definitive excretory pores in the cercariae of the Prosostomata is variable. In some families, the pores are at the junction of the body and tail and in others on the sides of the tail at varying distances from

the body. In a few groups, the pores are well toward the posterior end of the tail and thus approach the situation described above for *C. laevicardii*. In the Strigeatoidea, the excretory vesicle of the cercaria is always thin-walled, whereas in the Prosostomata it may be either thin- or thick-walled, the latter condition being evidently a secondary one. These facts and many others beyond the scope of a brief discussion suggest that as a group, the Strigeatoidea is more primitive than the Prosostomata. Yet the two orders have so much in common that their having arisen independently from turbellarian stock is inconceivable; their point of divergence must have been considerably removed from that source. It may be doubtful whether the Fellodistomatidae is the extant group closest to such a point of divergence but at least present knowledge of that family affords a plausible explanation of how the larvae of one order could have arisen from those of the other. In this connection, it is of interest to note that in the Fellodistomatidae the genital pore of the adult is anterior to the ventral sucker whereas in other families of the Strigeatoidea it is either at the extreme posterior end of the body or closer to that end than to the anterior extremity except in some blood flukes. Thus in respect to the location of this opening, the fellodistomatids are more like the Prosostomata than strigeatoids.

SUMMARY

Cercaria laevicardii sp. nov. is described from the marine lamellibranch, *Laevicardium mortonii*. The cercaria develops in simple sporocysts and is similar to the larva of *Bacciger bacciger*. The excretory formula is $2 [(3 + 3) + (3 + 3)]$ and the structure and development of the excretory system is such that the larva is interpreted as having been derived from the furcocercous type. Various caudal modifications in fellodistomatid cercariae are discussed and the possible phylogenetic significance of some types is mentioned.

LITERATURE CITED

- ALLISON, L. N., 1943. *Leucochloridiomorpha constantiac* (Mueller) (Brachylaemidae), its life history and taxonomic relationships among digenetic trematodes. *Trans. Amer. Micros. Soc.*, **62**: 127-168.
- CABLE, R. M., 1953. The life cycle of *Parvatrema borinquenae* gen. et sp. nov. (Trematoda: Digenea) and the systematic position of the subfamily Gymnophallinae. *J. Parasitol.*, **39**: 408-421.
- CHUBRICK, G. K., 1952. (The immature stages of the trematode *Fellodistomum fellis* Nicoll, 1909, from invertebrates of the Barents Sea.) (In Russian.) *Zool. Zhur.*, **31**: 653-658.
- DOLLFUS, R. P., 1925. Liste critique des cercaires marines à queue sétigère signalées jusqu'à présent. *Trav. Stat. Zool. Wimereux*, **9**: 43-65.
- JONES, E. I., AND M. ROTHSCHILD, 1932. On the sporocyst and cercaria of a marine distomid trematode from *Nucula*. *Parasitol.*, **24**: 260-264.
- LA RUE, G. R., 1926. Studies on the trematode family Strigeidae (Holostomidae) No. III. Relationships. *Trans. Amer. Micros. Soc.*, **45**: 265-281.
- LE ZOTTE, L. A., JR., 1954. Studies on marine digenetic trematodes of Puerto Rico: the family Bivesiculidae, its biology and affinities. *J. Parasitol.*, **40** (in press).
- PALOMBI, A., 1934. *Bacciger bacciger* (Rud.), trematode digenetic: fam. Steringophoridae Odhner. Anatomia, sistematica e biologia. *Pub. Staz. Zool. Napoli*, **13**: 438-478.